

Synonymy of the Genus *Occipitalia* Richards, 1978, with *Clypearia* de Saussure, 1854 (Hymenoptera: Vespidae; Polistinae, Epiponini)

JAMES M. CARPENTER, JOHN W. WENZEL AND JUN-ICHI KOJIMA

(JMC) Department of Entomology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024, USA; (JWW) Department of Entomology, Ohio State University, Columbus, Ohio 43210, USA; (JK) Natural History Laboratory, Faculty of Science, Ibaraki University, Mito 310, Japan

Abstract.—The genera *Occipitalia* and *Clypearia* are synonymized. The single species included in *Occipitalia*, *sulcata* (de Saussure), is the sister-group of *Clypearia*, based on morphological and behavioral characters. This species is intermediate in the morphological and nest architectural characters defining *Clypearia*. There is thus no useful reason to separate these genera.

In December of 1990, JMC and JWW collected six colonies and numerous individuals of the paper wasp *Occipitalia sulcata* (de Saussure) along the Amazon and Napo Rivers in Loreto, Peru. The collection included the hitherto undescribed male and larva of this species. The nests represent a larger sample than any previously available, and detailed study of nest architecture, along with adult and larval morphology, lead us to the conclusion that the genus *Occipitalia* Richards should be synonymized with *Clypearia* de Saussure.

TAXONOMIC HISTORY

Clypearia de Saussure, 1854, was described as a subgenus of *Polybia* Lepeletier for the single species *apicipennis* (Spinola, 1851). Ducke (1904: fig. 4) first described the nest of this species, noting its similarity to that of the genus *Synoeca* de Saussure. The nests of these taxa are what is now termed astelocytarus: with combs lacking pedicels, built directly on the substrate, and covered with an envelope. Ducke (1905a) first raised *Clypearia* to genus (Richards 1978: 191, cited Ducke 1905b), in part because of its nest architecture, on which basis he grouped *Clypearia*

with *Synoeca* and *Metapolybia* Ducke rather than *Polybia*. The nests of *Polybia* are termed phragmocyttarus: with a series of stacked combs, each having an envelope and built on the envelope of the preceding comb. Ducke (1906) described another species of *Clypearia*, *angustior*, and Araujo (1951) illustrated its nest and described the male. As noted by Richards (1978: 192), *Clypearia* is a "genus whose species are rather rare in collections," and it received little further attention in the literature until Richards' monograph, in which he described five new species. Since then, Jeanne (1979) figured the nest of *weyrauchi* Richards, Jeanne (1980) described meconium extraction in *apicipennis*, Jeanne *et al.* (1983) described sternal glands in this species, and Snelling (1983) and Sarmiento (1994) provided range extension records for *naumannii* Richards. The genus was discussed in the chapters by Carpenter, Jeanne, Wenzel, and Downing in the recent book, *The Social Biology of Wasps* (Ross and Matthews 1991).

In his monograph, Richards (1978) described the genus *Occipitalia* to include two species formerly placed in *Polybia*. These were *sulcata*, the type species, and *trailsi* Cameron. Richards justified the new

genus as follows (p. 198): "It has always been noted that *P. sulcata* and *P. traili* (*P. ujhelyi*) were very unusual species of *Polybia* but they were rare and nothing was known of their biology. Dr W. D. Hamilton found them in some numbers on the Amazon and discovered that the nests are astelocytarus, quite unlike any species of *Polybia* (all phragmocytarus). I think therefore it is appropriate that they should be generically separated since they also lack the pronotal fovea found in all other *Polybia*."

Richards' phylogenetic tree for the genera of Polistinae (his fig. 40) showed *Occipitalia* as most closely related to *Clypearia*, with both genera sharing the state of larval mandibles "rather long, two teeth" (9a in his table 1; the origin of this state is not unique on Richards' tree, but as discussed by Carpenter (1991), that diagram is not based on a parsimonious mapping of the characters presented by Richards. Note also that Richards described the larva of *Occipitalia* on p. 198 as "with one long apical tooth," contradicting both his tree and key to larvae). Richards grouped *Occipitalia* + *Clypearia* in a clade including *Synoeca* and *Metapolybia*, based on absence of the pronotal fovea, secondary spiracular entrance raised and narrow, and nests astelocytarus.

Snelling (1981) treated *Occipitalia* as a synonym of *Polybia*, stating only (p. 374) that he did not consider it "sufficiently distinct from *Polybia*." That action was certainly unjustified. But then Raw (1985) split *Occipitalia*, describing the new genus *Asteloea* for *traili*. Raw stated (p. 185): "Morphologically, the two species are quite different so I compared them with related genera. The genus is not monophyletic, but neither of the two species is sufficiently close to any recognized genus to justify a transfer." Raw considered that *Occipitalia* and *Asteloea* formed "a natural group" with *Synoeca*, *Metapolybia* and *Clypearia*, and compared 11 characters among these five genera. He did not discuss states

in other genera, but concluded (p. 187) that "*Asteloea* lies closer phylogenetically to *Metapolybia* than to *Occipitalia*." About the relationships of *Occipitalia* he came to no conclusions, although his table 1 showed it differing from *Clypearia* in only three characters, fewer than the four differentiating *Asteloea* and *Metapolybia*.

Carpenter's (1991) analysis of generic relationships in Polistinae established a monophyletic group comprising *Occipitalia sensu stricto*, *Asteloea*, *Clypearia* and *Metapolybia*, based on the raised pronotal prominence (= anterior pronotal carina; see Carpenter 1989), but did not resolve their interrelationships. The sister-group of these four genera is *Synoeca*, based on loss of the pronotal carina and astelocytarus nests. These five genera are a lineage within Epiponini, a tribe that comprises all of the neotropical polistines that found new colonies by swarms (Carpenter 1993). Wenzel's (1993) detailed analysis of nest architecture likewise recognized a lineage comprising these five genera; he did not detail the characters supporting this clade, but it was based on three features: comb built on bark without pulp foundation, material of coarse chips, and envelope reinforcement by secretion. His results differed from Carpenter's, which were based mostly on adult morphology, in placing *Synoeca* as sister-group of *Metapolybia*, with *Asteloea* most closely related in turn; relationships of *Occipitalia* and *Clypearia* were not resolved further. Wenzel and Carpenter (1994) combined the data matrices from Carpenter (1991) and Wenzel (1993), and added unpublished larval characters provided by JK; their analysis established *Occipitalia sulcata* and *Clypearia* as sister-groups. Characters supporting the branches were not detailed, but this relationship was based on six characters: tempora narrowed, forecoxa rounded, propodeal concavity broad and deep, metasomal segment I subpetiolate, two larval mandibular teeth with subsidiary tooth distinct, and comb heavily rein-

forced and obscuring initial construction. We now take up the matter of the distinction between *Occipitalia* and *Clypearia*.

ADULT MORPHOLOGY

Richards' (1978) concept of *Occipitalia* being a composite of what are now considered two genera, his keys and diagnoses do not accurately distinguish *O. sulcata* from *Clypearia*. The crucial character given in his generic key (p. 10, couplet 16), "Gena narrow even in ♀" vs. "Gena normal, wide at least in ♀," is more precisely described in his diagnosis of *Clypearia* (p. 191) as "Outer orbits (gena) very narrow, at top never more than half as broad as eye, below retreating and much narrower." His key to species of *Occipitalia* (p. 198) separates *O. sulcata* from *A. traili* by, *inter alia*, "Gena about half as wide as eye." To be sure, *O. sulcata* has the gena wider than any species of *Clypearia*, but it is narrower than is typical in other epiponines. As well, the state is variable within *Clypearia*, with *C. weyrauchi* having the gena wider than other species we have examined (*viz.*, *C. apicipennnis*, *C. angustior*, *C. duckeri* Richards and *C. naumanni*). Distinguishing *Occipitalia* from *Clypearia* on this basis is simply arbitrary partitioning of continuous variation. A similar situation for this particular character has been shown in the synonymy of *Pseudochartergus* with *Protopolybia* by Carpenter and Wenzel (1990).

Of the other characters discussed in Richards' diagnoses and keys, for only four are any differences at all stated between *O. sulcata* and *Clypearia*. These are, *seriatim*: (1) mandibles "rather long" in *Clypearia* vs. "short" in the composite diagnosis of *Occipitalia*. The mandibles of *Asteloeca* differ from *Clypearia*, not so much in length as in having the external margin drawn out into a flange; *O. sulcata* does not differ from *Clypearia*. (2) Clypeus "much longer than broad" in *Clypearia* vs. "about as wide as long" for *O. sulcata* in the key to species of *Occipitalia*. That dif-

ference holds, but again is continuous variation, with *O. sulcata* having the clypeus narrower than, say, *Asteloeca* (clypeus "much wider than long" in the same key). And again, the character is variable within *Clypearia*, with *C. weyrauchi* having the clypeus wider than the other species. Moreover, the clypeal apex is described as "feebly truncate" in both *Clypearia* and *O. sulcata*, a derived condition (*O. sulcata* having the truncation less pronounced and slightly narrower than in species of *Clypearia*), and the clypeal-eye contact in both is about as long as the width of the antennal socket. (3) Fore basitarsus "two and a half or (*C. angustior*) three times as long as broad" in *Clypearia* vs. "three and a half times as long as broad" in the composite diagnosis of *Occipitalia*. Again, this is continuous variation, and again even within *Clypearia*, and the character offers only an arbitrary basis on which to distinguish the two genera. (4) Metasomal segment I, which is of variable form in *Clypearia*; the petiole in *O. sulcata* is within this variation, similar in form to the petiole of *C. angustior*.

Occipitalia and *Clypearia* are thus at best poorly differentiated by the characters treated by Richards (1978). Taking up the characters listed by Raw (1985: table 1), of the three characters differentiating *Occipitalia* and *Clypearia*, two have already been discussed: #4, length of the clypeus, and #10, width of the gena (note that Raw listed an intermediate state for this latter character in *Occipitalia*). The remaining character, #3, whether the antero-dorsal edge of the propleura is folded out along its entire length or only in part, had only *Occipitalia* with the former state. The difference between this taxon and the others is minor at best, but in any case is simply an autapomorphy of *O. sulcata*.

Turning now to characters of the male, these show the usual sexual dimorphism in Polistinae—a statement that could replace most of the descriptions of males in Richards (1978). The antennae, clypeus,

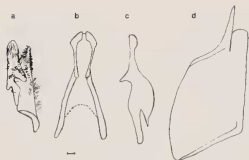


Fig. 1. Male genitalia of *Occipitalia sulcata*. a, volsella, lateral view; b, aedeagus, ventral view; c, aedeagus, lateral view; d, paramere, lateral view. The scale bar is 1 mm.

tempora, metasoma, and so forth, differ between the sexes *O. sulcata* in just the same way as is typical of other polistines. The more critical source of characters is male genitalia, and this character system was scarcely discussed in Richards' monograph. He briefly summarized (1978: 5) an unpublished survey of polistine genera by Vreugdenhil and van der Vecht, but the *Occipitalia* studied was *A. traili*. Of the species of *Clypearia*, males were known for only two, *C. angustior* and *C. duckei* Richards. Araujo (1951) published a photograph showing the genitalia of the former species in general aspect, but the genitalia of the single male specimen of the latter species were not studied by Richards. We have examined two species of *Clypearia* (*apicipennis* and *naumanni*) and the hitherto undescribed male of *O. sulcata*, as well as *Asteleoca*, all five species of *Synoeca*, and five of *Metapolybia* (*bromelicola* Araujo, *cingulata* (F.), *docilis* Richards, *suffusa* (Fox) and an undescribed species).

The male genitalia of *O. sulcata* are illustrated in Fig. 1, and those of *C. duckei* in Fig. 2. The genitalia of the genera examined are basically similar, with some differences in detail of the shape of the aedeagus noted. In particular, the aedeagus of *Synoeca* is more attenuate than in the other four genera. These latter genera have the aedeagus apically broader, and the cuticular rods which form the aedeagus are more strongly sclerotized. As-

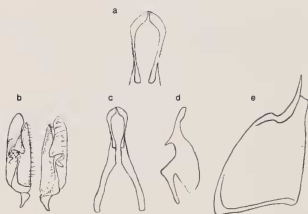


Fig. 2. Male genitalia of *Clypearia duckei*. a, apex of aedeagus, ventral view; b, volsella, lateral view; c, aedeagus, ventral view; d, aedeagus, lateral view; e, paramere, lateral view. The scale for b-e is the same as Fig. 1; a is drawn at about twice that magnification.

sessing the significance of this character will require thorough investigation of the other genera of Epiponini: it may be an autapomorphy of *Synoeca*, or else support the monophyly of a group comprising the other four genera. In any event, the male genitalia do not support the distinction of *Occipitalia* and *Clypearia* (cf. Figs. 1 and 2). Aside from the aedeagus, the only notable feature is the volsella of *S. surinama*, which has the digitus much more sharply pointed ventrally than any of the other species, an evident autapomorphy.

Regarding the three characters of the male genitalia mentioned by Richards (1978: 5) as distinguishing two groups of genera, the genitalia of *O. sulcata* fall into Group II (as do the other genera discussed here). However, the two groups are not distinct as stated. First, as shown in Fig. 1, Group II genitalia may have the aedeagus "serrate" beneath; the serration is simply very fine. Second, the medial lobes of the aedeagus (ventral process of Richards) differ in shape and size, rather than attachment to the cuticular rods. But it is not clear how, if at all, the two groups may be distinguished by the medial lobes, for these show considerable variation. And concerning the third character, hairs on the parameral spine, these are lacking in *O. sulcata* and the other genera examined

here. But this feature varies within Group I (*viz.*, a few short hairs in *Parachartergus*). The distinction of the two groups should be re-examined in the context of a comprehensive investigation of all the polistine genera, a task we will take up elsewhere.

LARVAL MORPHOLOGY

Richards' (1978) key and description of the larva of *Clypearia* was based on a single species, *C. duckei*. He did not state on which species his description of *Occipitalia* was based, but it was *A. traili*, according to an unpublished manuscript preserved in the British Museum (Natural History). JK has studied the larva of *O. sulcata*, and it and *C. duckei* have the same condition of two larval mandibular teeth, with the subsidiary tooth distinct (secondarily derived condition). This is a synapomorphy between these two taxa. The only differences among the remaining larval features studied are: (1) setae on the cranium are very sparse and minute in *C. duckei* and are thick bristles in *O. sulcata*, the latter condition being more derived; (2) setae on the venter of thoracic segment I through abdominal segment I are thin and short in *C. duckei* vs. thick bristles in *O. sulcata*, the latter condition again being more derived; and (3) body spicules on anterior four or five segments are blunt or minutely dentate in *C. duckei* vs. pointed in *O. sulcata*, the former state being derived. These characters are often polymorphic or variable within other polistine genera, and so we view these differences as minor, having no more than specific value.

NEST ARCHITECTURE

As already mentioned, the nests of several species of *Clypearia* have been described and illustrated. The nest of *O. sulcata* has also been illustrated; as noted by Richards (1978: 199), Evans and West-Eberhard (1970: fig. 92, not 85 as stated by Richards) figured its nest as "*Clypearia* sp."

Similar nest architecture has been regarded as evidence of close relationship by authorities on Polistinae (see, e. g., de Saussure 1853–1858; Ducke 1914; Richards 1978). Much of this view is now supported by modern analytic methods whereas other aspects are not (Carpenter and Wenzel 1990; Wenzel 1991, 1993). The regions where classical views differ from modern views are generally those where taxa are poorly known or where concepts of the polarity of character state transformations are critical. Both of the genera in question here are still poorly known in comparison to other South American genera. Statements not followed by a citation are based on specimens in the private collection of W. D. Hamilton (*C. duckei* and *A. traili*), and specimens collected by JMC and JWW and deposited in the AMNH.

The relevant aspects of nest architecture are those of the neotropical taxa that build combs as sessile structures (no supporting pedicel), and subsequently expand the nest along the substrate contiguously with the primary comb (*astelocytarus sensu* Richards 1978) rather than by building a new comb upon the exterior of the primary envelope (*phragmocytarus sensu* Richards). *Polybia* builds nests of the *phragmocytarus* type, quite unlike those of the genera discussed here (*Asteloecca*, *Clypearia*, *Metapolybia*, *Occipitalia*, *Synoeca*). Although they are not all relevant to the morphological determination of the placement of *O. sulcata*, these latter five genera are discussed below because of overlapping architectural variation for which character polarity has yet to be determined. Taken in turn, the major elements of comparison are: the comb either entirely *versus* only partly attached to the substrate; the envelope thin and showing the original lines of construction *versus* later reinforced by addition of more pulp to the surface; and the structure of the nest entrance.

If the support is broad, the initial comb will be built entirely sessile upon it. If the

support is a narrow branch, *C. duckei*, and *A. traili*, project a planar comb beyond the margin of the branch, a trait that is probably plesiomorphic given that it is also found among many phragmocytarus genera (Wenzel 1991: figs. 48–58). In contrast, *Metapolybia* and *Synoecca* will wrap a comb around a narrow branch so that all cells have their bases on the substrate, as perhaps will *C. angustior* (Araujo 1951). *O. sulcata* and *C. apicipennis* are intermediate between these extremes. Nests of *O. sulcata* will wrap partly around a narrow support before being extended beyond it. One specimen from near Iquitos, Peru (AMNH 901231–1), has cells around nearly half the circumference of a branch; however, these cells are oriented through only about 90 degrees relative to each other, rather than representing radii of the curve, and the bases of yet more lateral cells are built free of the substrate. Very similar to this is *C. apicipennis*, which builds all brood cells sessile on the branch, inside a bulging envelope. The space between the brood comb and the envelope is filled with structural, non-brood “cells” (Jeanne, pers. comm. to JWW).

Nests of *C. duckei* and *O. sulcata* are built of a rough carton. The envelope rises abruptly from the substrate and is reinforced and disguised by subsequent addition of many fine particles that may differ in color and shape from the original carton (a trait widespread among epiponines), but *C. duckei* envelope may also have windows of pure secretion elsewhere. In contrast, both nests of *C. weyrauchi* collected by Jeanne (1979) and Weyrauch (now in the Fundación e Instituto Miguel Lillo, Tucumán, Argentina, and strikingly similar to that photographed by Jeanne) had envelopes that arose at a shallow angle from the substrate and were composed of fine, straight parallel lines of construction. *C. weyrauchi* and *A. traili* build a very smooth envelope that is glossy and thoroughly covered with secretion after completion. Intermediate be-

tween these two pairs of species, a nest of *C. angustior* was built by application of pulp in tortuous, fine stripes, short and spread in all directions; although the surface was rough, there were windows that consisted of pure secretion with no pulp (Araujo 1951: 55). This description would fit most *Metapolybia* nicely. When the back of the comb projects beyond the support, *C. duckei* and *O. sulcata* thicken it with pulp, obscuring cell bases. The comb sides are also thickened and do not show cell contours, and the cells may be partly flattened so as to provide a smooth exterior wall (*C. duckei*). In contrast, the exterior of a *C. angustior* nest (which did not project beyond the support) was reported to reflect the positions of cell walls (Araujo 1951), as does that of *A. traili* (which does project), and often *Metapolybia* and *Synoecca*. Jeanne's *C. apicipennis* did not have an envelope in contact with the walls of the brood cells (above), and there was no evidence of secondary thickening of the envelope anywhere (Jeanne, pers. comm. to JWW). *C. weyrauchi* (entirely sessile on the substrate) envelopes do not contact the cells. The *Asteloecca* nest collected by JMC and JWW (AMNH) and one recorded by W. D. Hamilton (unpublished notes) indicate that *A. traili* is unique among these species in that the comb back is extended beyond the substrate, but not reinforced by additional pulp, so that rows of convex cells bottoms are clearly visible.

In all astelocytarus genera, expansion of the nest is accomplished by adding a new comb adjacent to, and contiguous with, the older comb. *Synoecca virginea* will sometimes build cells on the envelope (van der Vecht 1967; Overal 1982), but this is not known as a regular habit among the other *Synoecca* or other genera considered here. Richards' (1978: 199) statement regarding *Occipitalia* that “at a later stage cells were built on the envelope and covered with a new one” is based on notes by R. L. Jeanne, who is of the opinion that these cells were not normal and not part

of the regular comb that expands along the branch (Jeanne, pers. comm. to JWW). Ducke (1910) said that his nest of *C. apicipennis* was enlarged like *Synoecca*, but with additions more irregularly juxtaposed, and his photograph shows a nest growing in several sections along a branch. When *Synoecca* and *Metapolybia* build on an inclined surface, the expansion is directed upward. The new structure generally encompasses the original entrance hole (which is at the periphery of the envelope in the upper part of the nest), concealing it. In these two genera, the entrance is built as a short collar and is built separately from the last gap in the incipient envelope. *C. angustior* (Araujo 1951) and *C. duckei* both build short collars, the former peripherally and upward, the latter at least peripherally, perhaps directed upward (it is not yet known how these structures relate to the last gap in construction). In contrast, *C. apicipennis* has an entrance at the top, but without any collar or spout (Jeanne, pers. comm. to JWW). *O. sulcata* and *C. weyrauchi* have no collar or spout at the entrance, which in both cases is the last remaining gap in construction and is more central rather than peripheral in the envelope. Neither Jeanne's (1978) nor Weyrauch's nest of *C. weyrauchi* showed evidence of expansion, but one nest of *O. sulcata* that was apparently expanded (AMNH 901231-4) had two entrances, one at the center of the old envelope and one at the center of the contiguous new addition, as would be expected if the new envelope does not overlap the old entrance. *A. trilli* has the entrance in the center of the envelope and built at the last remaining gap, but it orients a short collar downward.

Finally, two other behavioral traits are noteworthy and deserve more attention. First, all of the six *O. sulcata* colonies JMC and JWW collected (and the several more they did not) were in close association with the nests of *Azteca* ants, sometimes only centimeters away. Hamilton (1972:

225), Richards (1978: 199, discussing nests collected by Hamilton) and Chadab (1979: 162) have all commented on the association, which appears to be obligate. It would be interesting to know to what extent the species of *Clypearia* share this trait; evidently *C. apicipennis* and *C. weyrauchi* do not, but Richards' (1978: 196) description of *C. duckei* gave label data as "in ant complex" and Chadab (1979: table 49) listed this species as nesting with *Azteca* in Limoncocha, Napo Province, Ecuador. Secondly, some of these species remove the meconium through the mouth of the cell after an adult emerges (Jeanne 1980). Jeanne's study found that such hygienic behavior was present in *C. apicipennis*, *O. sulcata*, and *A. trilli*, but not in *C. weyrauchi*, and evidently not in *Synoecca* or *Metapolybia*. At the time of Jeanne's publication, Richards had recently placed *O. sulcata* and *A. trilli* in his new genus *Occipitalia*, so the fact that they shared this trait made more sense than it does now in light of what we propose to be a rather distant relationship between them.

The evidence from nest architecture is somewhat ambiguous as to the correct placement of *O. sulcata*, but several things are clear. The range of variation found in *Clypearia* for architectural traits (such as attachment to the substrate, reinforcement of original carton, and placement and structure of the nest entrance) includes the states typical of *O. sulcata*. Indeed, the species of *Clypearia* appear to have no unique synapomorphy among these traits to distinguish them from *O. sulcata*. Furthermore, *A. trilli* is not more closely allied to *O. sulcata* than to *Clypearia* species, contrary to Richards' opinion, and would be placed awkwardly anywhere among the known forms.

CONCLUSION

We have documented that there is no adequate basis, in adult or larval morphology or nest architecture, for separating *Occipitalia* from *Clypearia* at the generic

level. Regarding adult morphology, the features by which these genera differ are nothing more than the arbitrary partitioning of continuous variation. For the larvae, there are only minor, specific differences between the two species known. And nest architecture does not differ.

Richards (1978) was correct to remove *O. sulcata* and *A. traili* from *Polybia*. But his original concept of *Occipitalia* was not monophyletic, instead it was a composite of two distantly related species. Raw (1985) correctly separated *A. traili* from *Occipitalia*; as concluded by Raw and shown in Wenzel and Carpenter (1994) *A. traili* is more closely related to *Metapolybia*, as established by the synapomorphies of mandibular edge raised, first metasomal tergum abruptly expanded apically, and thyridium elongate. But with the recognition of *Asteloea*, the distinction between *Occipitalia* and *Clypearia* is also largely removed. Synonymy of these two genera is thus indicated, and we establish that synonymy now.

Clypearia de Saussure, 1854: 165, as subgenus of *Polybia* Lepeletier, 1836.

Type species: *Polistes apicipennis* Spinola, 1851, by monotypy.

Occipitalia Richards, 1978: v, 11 (key), 198, as genus. NEW SYNONYMY.

Type species: *Polybia sulcata* de Saussure, 1854, by original designation.

Occiitalia [!] Richards, 1978: 16. Incorrect spelling of *Occipitalia*.

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with the CorelDraw program. We are pleased to have the opportunity to publish some more of van der Vecht's work.

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